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# BIOLOGICAL BULLETIN

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## THE BREATHING AND FEEDING MECHANISM OF THE LAMPREYS.<sup>1</sup>

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The present study of the respiratory mechanism of the lampreys was undertaken at the suggestion of Professor Jacob Reighard and has been carried out under his direction. Preserved material of *Petromyzon marinus* Linnæus, *Petromyzon marinus unicolor* (De Kay) and *Lampetra wilderi* Gage has been examined, but these three species have been found to be so nearly alike in the structure of their respiratory mechanism that the following anatomical description of *Petromyzon marinus* holds good in all essentials for the other two species. Where measurements are given they are taken from *P. marinus* and refer to individuals of average size. The close relation between feeding and breathing in the lamprey has made it necessary to consider the mechanisms of the two together. There is without doubt a similar close relation between the mechanism of respiration and that of circulation but this has not been included in the scope of the present paper.

### I. STRUCTURES INVOLVED IN BREATHING AND FEEDING.

Food entering the funnel-shaped cavity of the oral hood passes thence at the apex of the oral hood into the mouth cavity

<sup>1</sup> Contributions from the Zoölogical Laboratory of the University of Michigan, No. 92.

(Fig. 1, *b*). From the mouth cavity it passes through a constriction into the larger so-called pharyngeal cavity (*d*). From the pharyngeal cavity food enters the alimentary canal proper by way of the slender œsophagus (*p*) while water may conceivably enter the much larger water tube (*s*). The latter lies ventral to the œsophagus, extends caudad to the pericardial cavity, and there ends blind. Should water enter it from the pharynx it could then pour through the seven openings on each side into the gill sacs, from which it could reach the exterior by the seven external branchial openings on each side of the body (Fig. 5, *h*).

The opening from the pharynx into the water tube is guarded by a pair of velar valves (Fig. 1, *l*; Fig. 13, *l*), while valves guard also the external branchial openings (Fig. 13, *c*, *b*). Muscles control the opening between mouth cavity and pharynx and between pharynx and œsophagus. In order to understand the mechanism of these parts, each must be considered in greater detail.

*A. Oral Funnel, Mouth Cavity and Tongue.*—The oral funnel opens upon the ventral side of the anterior part of the head. In the specimens examined the average diameter of its external opening is 3.5 cm., while its dorsal opening, where it becomes continuous with the mouth cavity, has a diameter of 1 cm. Around the smaller opening of the funnel, on the boundary between it and the mouth cavity, is a supporting ring of cartilage, called the annular cartilage (Fig. 1, *t*). Attached to this cartilage and forming the muscular walls of the funnel is a three-layered muscle, the annularis (Fig 1, *u*). Fürbringer (1875) reports that the outer and middle layers of the annularis serve to attach the animal by the oral funnel while the inner layer causes the walls of the funnel to expand and contract, and this, together with the simultaneous closing of the mouth opening (opening between the oral funnel and mouth cavity), gives the animal power to suck blood or tissue which it has succeeded in rasping from its prey. The walls of the funnel become thin abruptly at their external edge, and there bear a thick fringe of rather short tentacles (Figs. 1, *i*; Fig. 2, *i*).

The posterior wall of the funnel forms with the ventral wall of the mouth cavity an angle of almost 90 degrees; the anterior

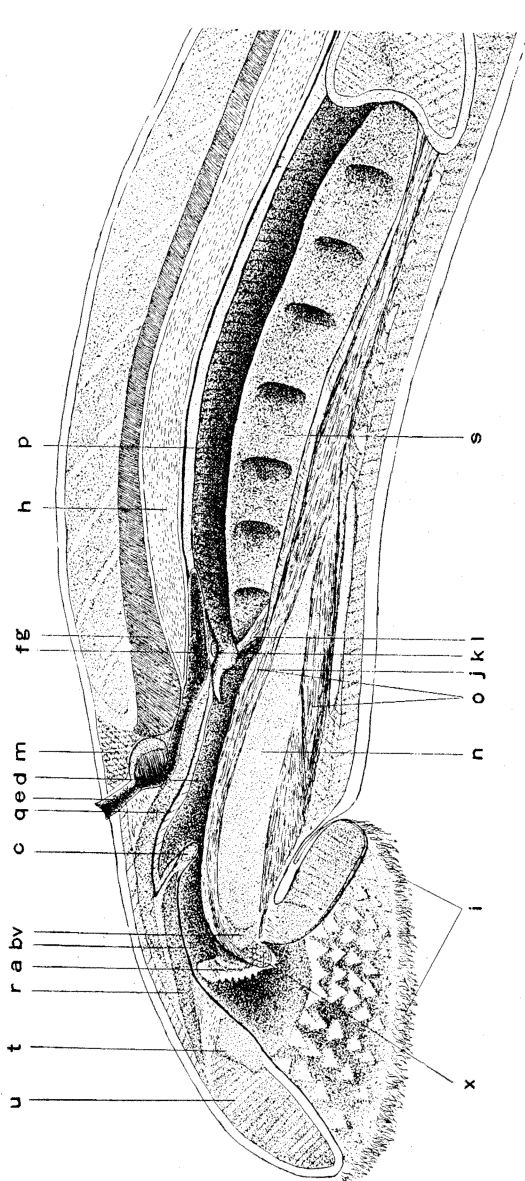


FIG. 1. Median longitudinal section through the head of *L. marinus*. *a*, tongue; *b*, mouth cavity; *c*, semiannularis muscle; *d*, pharynx; *e*, nasal tube; *f*, nasal cecum; *g*, brain; *h*, notochord; *i*, buccal fringe; *j*, velar jaw; *k*, posterior pharyngeus muscle; *l*, velar valve; *m*, connective tissue surrounding the epiphysis; *n*, lingual cartilage; *o*, muscles of tongue; *p*, cesophagus; *q*, ethmoid cartilage; *r*, semiannularis cartilage; *s*, water tube; *t*, annular cartilage; *u*, annularis muscle; *v*, central cartilage of the tongue; *x*, anterior lobe of the tongue.

wall meets the dorsal walls of the mouth in a much gentler curve.

The funnel is lined with thick mucous membrane bearing sharp conical teeth (Fig. 2). The teeth are arranged in a series of concentric loops, the crossed ends of which lie in the anterior portion of the funnel (Figs. 1 and 2). The result of this arrangement is that any radius drawn from the center of the mouth opening strikes at least two teeth except over the posterior one fourth of the circumference of the funnel. This posterior one fourth of the funnel has teeth approximately on radii running from that portion on the central loop which has an arc of the smallest

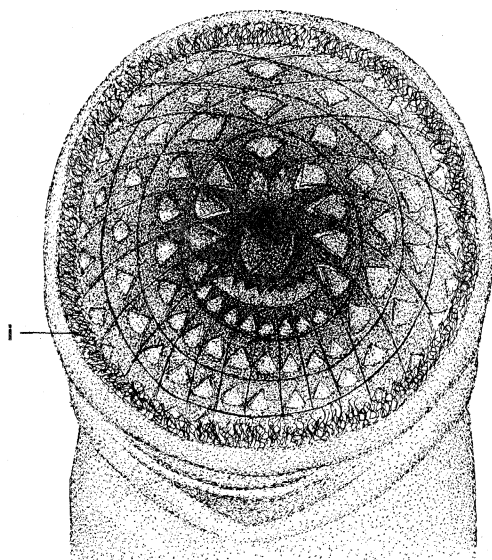


FIG. 2. Mouth of *P. marinus* showing the arrangement of the teeth in concentric loops.

radius. This is a necessary result of the geometric relation of the concentric loops (Figs. 2 and 3). The teeth on the central loop are so crowded that there are as many as on the larger outer loop. These teeth are also larger and are grown together in plates of two and more.

The end of the tongue (Fig. 1, Fig. 5 and Fig. 6) has two lateral lobes (*a*) which are covered with smooth mucous membrane and an anterior lobe (*x*) covered with plates of sharp teeth. This free end of the tongue may be seen projecting for 1 or 2 mm. into the caudal end of the funnel and the teeth on its ante-

rior lobe are thus brought into the same plane as the central teeth of the funnel and function with them in rasping. The great freedom of movement of the end of the tongue necessary in rasping is attained by its central cartilage (Fig. 1, *v*) being attached by a sort of socket joint to the enlarged anterior end of the large lingual cartilage (Fig. 1, *u*).

The mouth cavity is short and curved, about five times as long as it is wide at its middle, and extends from the oral funnel to the pharynx, a distance of about 2 cm. Its anterior end, where it meets the funnel, is larger than in any other part. Its roof and

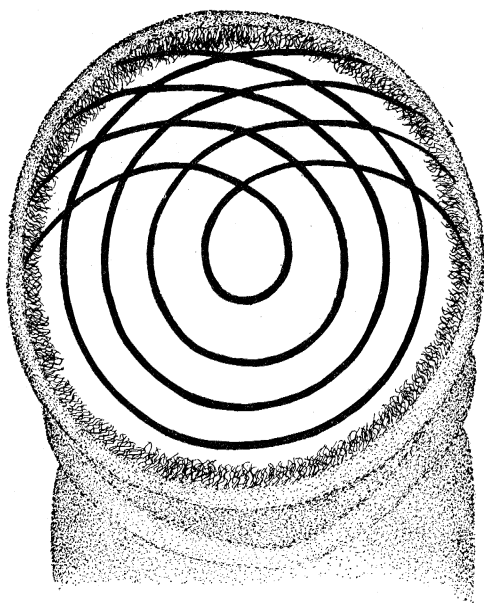


FIG. 3. Diagram of the arrangement of the teeth in the oral funnel of *P. marinus*. The heavy lines show the loops upon which the teeth are inserted.

sides are dome shaped and are formed by the semiannularis cartilage in front and by the semiannularis muscle behind (Fig. 1, *r*, *c*). The muscle arises from the posterior border of the cartilage and forms a very small portion of the roof of the mouth. The posterior portion of the dome formed by the semiannularis muscle arches so close to the ventral wall of the mouth that it greatly constricts the cavity in this region and when it contracts, completely shuts off the mouth cavity from the pharynx. The floor

of the mouth is formed by the large underlying tongue muscle (Fig. 1, *o*). The tongue as a whole is a large, long cone which stretches from the mouth opening to the ventral anterior portion of the pericardium to which it is attached by its apex. Thus the tongue underlies the whole mouth cavity, pharynx, and water tube. When the tongue is pushed forward so that its lobes occupy the flaring anterior part of the mouth cavity, its lateral lobes fall apart (Figs. 5, 6) and there is left between them a passage-way which connects the cavity of the oral funnel and that of the mouth. This passage-way, which then has a cross section equal to that of the mouth cavity at its middle, diminishes rapidly in diameter as the tongue is drawn back into the narrower part of the mouth cavity until at last it is completely closed before the tongue has reached the posterior end of the semiannularis cartilage. The end of the tongue is thus seen to act as a piston working with a short stroke back and forth in the mouth cavity, the walls of which form the cylinder while the free end of the tongue forms the piston-head and its lateral lobes the valves.

B. *Pharynx*. — Passing out of the mouth cavity through the small opening ventral to the semiannularis muscle, the food enters the cavity of the pharynx. This cavity is somewhat irregular (Fig. 1, *d*). Its dorsal anterior portion is wedge-shaped in longitudinal section and extends forward over the semiannularis muscle and semiannularis cartilage. This portion of the pharyngeal cavity thus lies dorsal to the posterior portion of the mouth cavity. The remainder of the pharyngeal cavity is about 2.5 cm. in length from where it joins the mouth cavity to where it opens into the œsophagus and water tube. Instead of having a wall whose mucous membrane lies directly upon the tongue muscles on the ventral side and against the cartilage on the dorsal side, as in the case of the mouth cavity, there is, in the wall of the pharyngeal cavity, a thin layer of muscular tissue, the pharyngeus muscle intervening between the mucous membrane and the outer layers of muscle or cartilage. The pharyngeus (Fig. 4, *c*), which is fully described by Fürbringer (1875), entirely envelops the pharyngeal cavity and ends on a raphe on the mid-ventral line of the cavity. It is in contact with the mucous membrane except in the ventral lateral part of the

pharynx. Here between the pharyngeus muscle and the mucous lining of the cavity on its lateral walls are stretched two muscles, the hyomandibulari-semiannularis and the hyomandibulari-glossus. These muscles cause the mucous membrane to project

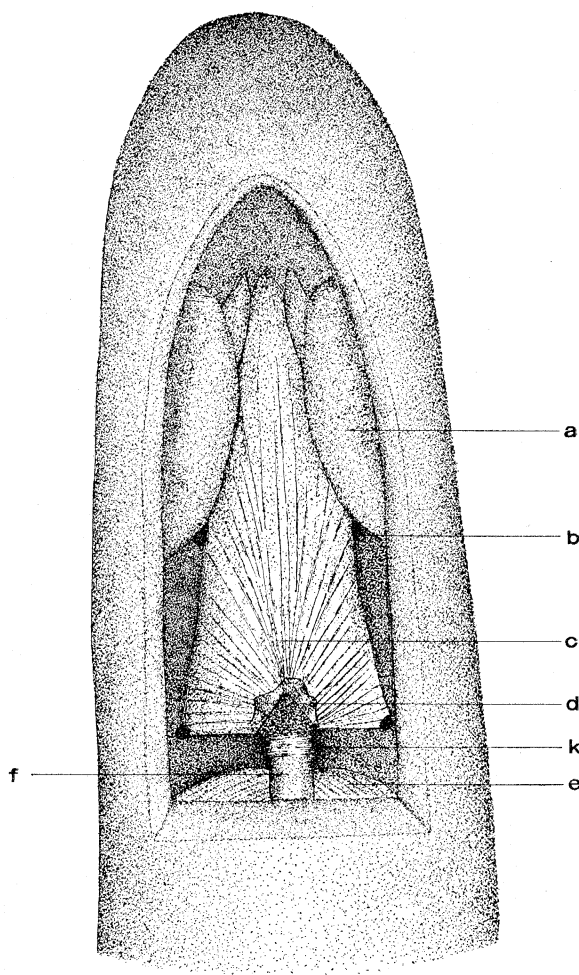


FIG. 4. Dorsal side of the head of *P. marinus* dissected to show the muscles overlying the pharynx and oesophagus. *a*, basilaris muscle; *b*, supporting cartilage; *c*, pharyngeus muscle; *d*, raphe of pharyngeus muscle; *e*, gill sac; *f*, oesophagus; *k*, posterior pharyngeus.

into the cavity in the form of a longitudinal ridge on each side.



The position of these muscles explains the difference between the size of the pharyngeus muscle viewed from the dorsal side (Fig. 4) and the actual size of the pharyngeal cavity (Figs. 1 and 5).

The outer supporting walls of the pharyngeal cavity outside of the pharyngeal muscle are: on the ventral side, the large tongue muscle; on the dorsal side, the ethmoid cartilage; on the anterior one half of the lateral walls, the basilaris muscle which expands and contracts the anterior half of pharyngeal cavity; lying dorsal to the basilaris muscles are found the large salivary glands which when the muscles act cause, according to Fürbringer (1875), a great flow of saliva.

The posterior pharyngeus is a strong bundle of muscular fibers arching over the mouth of the œsophagus between the walls of the nasal canal and that of the œsophagus (Fig. 1, *k*, and Fig. 4, *k*). This muscle lies just posterior to the pharyngeus muscle and when contracted closes off the œsophagus completely from the pharynx. When food reaches the posterior part of the pharynx, this muscle must relax to allow the food to pass on its way to the intestine.

The mucous membrane on the dorsal wall of the pharynx is continuous with that on the dorsal wall of the œsophagus, while that on the ventral wall is continuous with that on the ventral wall of the water tube. The ventral wall of the œsophagus and the dorsal wall of the water tube begin where the pharynx ends and continue caudad in close contact, parallel with the long axis of the body, to where the water tube ends, just anterior to the pericardium (Fig. 1). At the extreme anterior edge of the united walls of the pharynx and water tube there projects forward a pair of jaws which, on account of their connection with the velar valves, may be called velar jaws (Fig. 1, *j*; Fig. 5, *j*; and Fig. 6, *j*). They extend into the posterior part of the pharyngeal cavity and look like the jaws of a beetle. So close is the resemblance that at first sight one easily imagines that the animal has by some means swallowed a beetle, the jaws of which are lying in the pharynx. In Fig. 4, these jaws would lie beneath the triangular raphe (*d*).

The jaws are smooth and glossy and are covered with mucous membrane. Each is thick at the base where it unites with the

other and quite rapidly tapers to its point. The space between the jaws when they are open is a broad but incomplete ellipse ; when closed, the points of the jaws come together forming an entire but narrower ellipse.

The jaws extend forward from the free end of the united walls

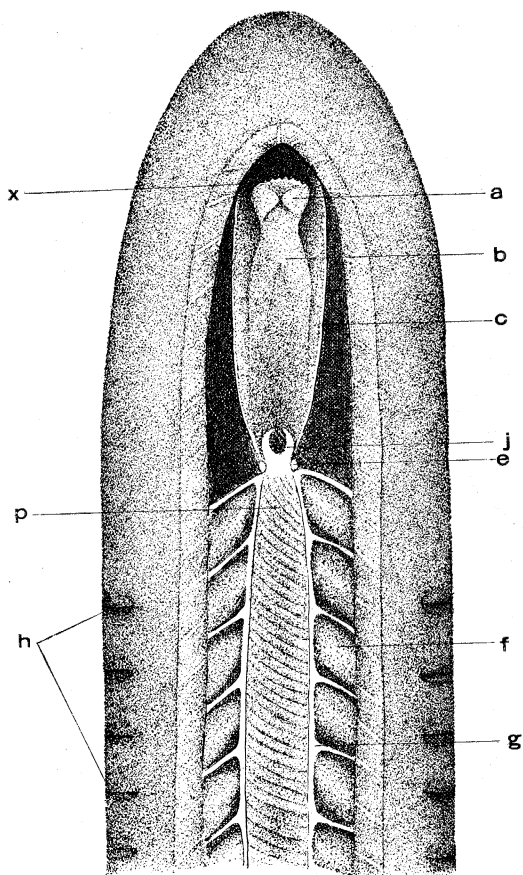


FIG. 5. Dorsal view of the head of *P. marinus* dissected so as to expose the cavities of the pharynx and œsophagus. *a*, lateral tongue lobe ; *b*, tongue ; *c*, pharynx ; *j*, velar jaws ; *e*, posterior pharynx ; *f*, gill sac ; *g*, gill pouch ; *h*, external branchipore ; *p*, œsophagus ; *x*, anterior lobe of the tongue.

of the water tube and œsophagus and in the same plane so that the greater part of their bulk lies ventral to the œsophagus. The position is not clearly shown in Fig. 1. The plane of the jaws is moreover oblique to the long axis of the pharynx which dips

ventrad to join the œsophagus and water tube. It results that the jaws extend obliquely across the opening from pharynx to water tube so as to intercept anything passing into the water tube. Nothing further can be seen of this apparatus from the pharyngeal cavity, but if the water tube be opened from the ventral side the velar jaws may be seen in connection with the velar valves

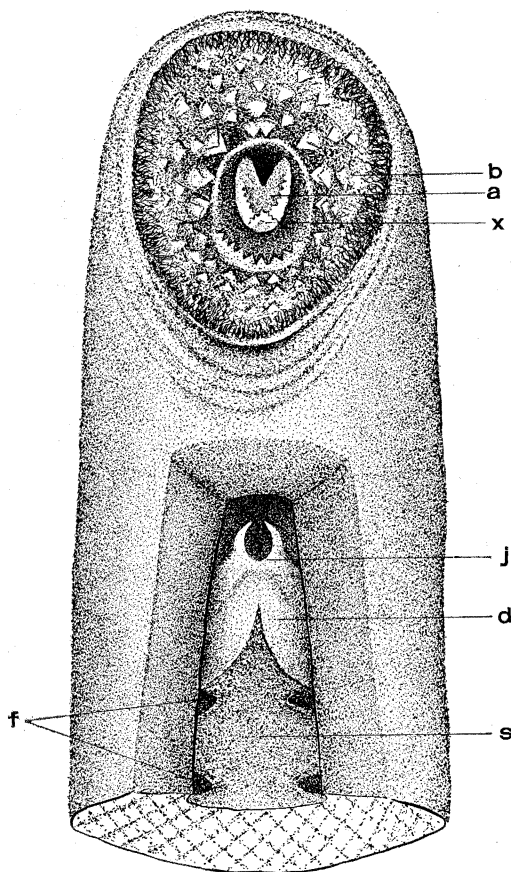


FIG. 6. Ventral view of the head of *P. marinus* with the cavity of the water tube and pharynx exposed. *a*, tongue; *b*, oral funnel; *d*, velar valves; *f*, internal branchiopores; *j*, velar jaws; *s*, water tube; *x*, anterior lobe of the tongue.

which guard the passage between the pharynx and water tube (Fig. 6). The velar valves (Fig. 1, *l*, and Fig. 6, *d*) are two semilunar flaps which extend dorso-ventrally, one on either side

of the water tube at its junction with the pharynx. They are united to one another in the middle line for 1 or 2 mm. near their dorsal ends but are free elsewhere, so that there is left between them a slit-like opening. They are concave caudally and their lateral edges are united to the water tube. They function normally to prevent water entering the pharynx from the water tube.

In order to understand the relation between the velar jaws and the velar valves the cartilaginous frame-work common to the two must be carefully dissected out. It is found to bear a striking resemblance to a pair of mechanic's nippers except that it is in one piece, whereas the latter is in two pieces. The jaws of this nipper-shaped cartilage are much smaller than the handles and have a much smaller arc between them. In fact the proportion between the jaws and handles of the cartilaginous apparatus is much the same as is found in the manufactured tool and like it tends to power in grasping. Approximation of the handles of a pair of nippers brings the jaws together. This is due to the fact that the halves of the nippers are crossed and fastened together by a pin. The two halves of the nipper-shaped cartilage are not crossed, hence when the handle is pushed inward, the corresponding jaw moves outward. The jaws of these nipper-like cartilages form the supporting skeleton of the velar jaws found in the pharynx, while the handles extend into the lateral walls of the water tube as slender cartilages which end on its ventral wall just cranial of the first internal gill opening (Fig. 6). The cartilages lie along the lateral attached edges of the velar valves and support them.



FIG. 7. Cartilaginous skeleton of the velar jaws and valves.

There are three pairs of muscles which are inserted into the nipper-shaped cartilage common to the velar jaws and velar valves. These are the *velo-pharyngeus*, *velo-hyomandibularis internus*, and the *velo-hyomandibularis externus*. They are sufficiently described by Fürbringer (1875), although he does not mention the velar jaws. Their combined action is to move the cartilaginous rods supporting the velar valves (the handles of the nippers) inward and outward. When the rods are moved inward, toward

one another, the velar valves are relaxed and water may pass from the water tube into the pharynx ; at the same time the velar jaws are opened. When the rods are separated, the valves are stretched so that they are able to close and the velar jaws are also closed.

C. *Gills*. — In order to get a clear idea of the gills it is necessary to call to mind their supporting skeleton. This consists of nine irregular vertical bars on each side. The first is placed almost immediately posterior to the styloid cartilage, the second immediately in front of the first gill cleft and the remaining seven are one just behind each of the seven gill clefts. These bars lie close to rings of cartilage, which surround the gill clefts but the bars are not continuous with the rings (Fig. 14). The vertical bars are united by four longitudinal bars ; one is placed above the gill clefts and one below them, while a third lies along the side of the notochord ; the fourth lies close along the mid-ventral line and is connected with the corresponding bar on the opposite side. The cartilaginous pericardial capsule is connected with the ventral longitudinal cartilages at their caudal end and is very elastic. This whole basket lies external to the gill sacs. While it yields to every muscular contraction, yet it is strong enough to lend firm attachment to muscles.

Lying within this frame-work are found the gill sacs. Each gill sac is a somewhat flattened ellipsoid. It is perforated at the ends of its major axis by the external and internal branchial openings. Its shortest axis is caudo-cranial so that we may conveniently distinguish in each sac a caudal and cranial surface or wall, a lateral and medial end, and a dorsal and ventral border. These sacs are not themselves attached to the supporting cartilage, but each lies within a muscular pouch to which it is connected by muscular fibers, and this muscular pouch is in turn attached to the cartilaginous rods of the visceral skeleton on three sides, dorsal, ventral and lateral.

The openings of the gill sacs into the water tube (internal branchiopores) have slightly swollen lips. Those belonging to each pair of sacs are in the same transverse plane. The opening of each pair of gill sacs to the exterior (external branchiopores) lie also in the same transverse plane, but in a plane caudal to

that which passes through the internal openings of the same pair of sacs. The principal axis of each gill sac, the axis connecting the branchiopores, is thus oblique to the long axis of the body and is directed from its medial end, caudo laterad (Fig. 5, *f*). The gill sac also crosses its muscular pouch obliquely. Its internal opening lies near the cephalic margin of the medial end of the pouch, while its external opening lies near the caudal margin of the lateral end of the pouch. The muscular pouches are larger than the gill sacs, so that the two lie in contact only at their openings, where they are united (Figs. 5 and 8).

When the gill sacs are examined from the outside, the lines of attachment of the gill lamellæ are seen (Fig. 8). While the walls of the gill sacs are thus transparent, they are nevertheless covered with a layer of muscle fibers (Fig. 8). These fibers are very delicate and form a thin layer which spreads over the gill sac like a spider's web and might easily escape notice. There are two of these muscles on each side of the sac. They have not hitherto been described. One muscle, the *external compressor of the gill sac* (Fig. 8, *f*), is a narrow band near the external opening of the sac. Its fibers arise from the lateral one fifth of the dorsal and ventral border of the gill sac and form over its surfaces arches with their concavities toward the external opening. The muscle functions in compressing the external one fifth of the gill sac.

The fibers of the larger muscle, the *internal compressor of the*

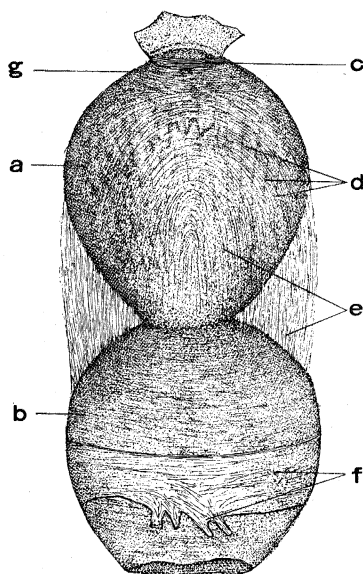


FIG. 8. Gill sac with its muscular pouch. The pouch is cut near its lateral end and reflected from the sac. *a*, gill sac; *b*, gill pouch; *c*, ental muscle; *d*, lines of the gill lamellæ showing through the gill sac; *e*, internal compressor muscle of the gill sac; *f*, deep compressor muscle of the gill pouch; *g*, external compressor of the gill sac.

*gill sac* (Fig. 8, *e*), arise on the medial one fifth of the dorsal and ventral borders of the muscular pouch. From this origin the fibers spread over the caudal and cranial surfaces of the gill sac not covered by the external compressor. They form arches whose concavities are directed toward the median plane. These muscles function to compress the gill sac while shortening its major axis.

The muscular pouches are placed side by side so that the cranial wall of each and the caudal wall of the next in front of it are in contact. So close do they lie that there appears to be but a single wall separating the contents of the successive pouches from one another (Fig. 5). Most writers indeed speak of the septa between the gill sacs without recognizing their double nature and the resulting muscular pouches. The double nature of these walls can be detected only by the microscope. They are very thin toward the center but become much thicker toward their borders. In preserved specimens a great abundance of coagulated lymph is found between the gill sac and its pouch. The muscular pouches are supported at their external openings by the small rings of cartilage already mentioned as lying close to the last seven vertical bars of the branchial basket (Fig. 14, *b*). These vertical and longitudinal bars of this basket lend support to the pouch on its lateral, dorsal and ventral walls. The medial wall is supported near its center by the wall of the water tube with which it is continuous and by cartilage at its extreme dorsal and ventral ends. These muscular pouches are placed in the cartilaginous basket very obliquely with the medial ends of the major axis craniad of the lateral ends. This added to the obliquity of each gill sac in its pouch causes the gill sacs to overlap each other like shingles on a roof. Nowhere can a cross section be made through the gill region without cutting two gill sacs. A line connecting the internal and external gill openings of any gill sac thus makes an angle of  $45^{\circ}$  with the long axis of the body.

The fibers of the muscular gill pouch are very difficult to follow on the outside of the pouch on account of the pigment found deposited there, but if the pouches be turned inside out, the fibers may be plainly seen crossing the flattened caudal and

cranial walls (Fig. 8). These fibers form arches convex toward the external opening and end on a narrow raphe on the dorsal and ventral walls of the pouch. The action of these muscles is to compress the whole muscular pouch and to cause its lateral end to be drawn toward the water tube thus greatly shortening its long axis and that of the gill sac.

On the inner surface of the gill pouch, at about the junction of the middle and lateral thirds of its major axis, are found strong bands of muscular fibers, *the deep compressors of the gill pouches*, lying beneath the fibers of the pouch proper. They arch in the same general direction as those already described and end on the dorsal and ventral borders of the pouch as do the muscle fibers of the pouch itself. In the center of the arch, however, some of the fibers run out diagonally toward the external gill opening and are attached to the surface of the gill sac at about the junction of the fourth and lateral fifths of its longer axis. They function in compressing the gill pouch and in fastening the gill sac to the pouch. These bands are found on both sides of the pouch, but are much larger on the cranial side. This may be due to the fact that the gill sac is so placed in its pouch that a greater space is found between the pouch and the sac on the cranial side than on the caudal side. On the caudal side of the internal opening may be seen many blood vessels (branches of the afferent branchial artery entering the gill sac) and these also serve to fasten the sac to the pouch at this point.

If a gill sac be turned inside out, the gill lamellæ may be seen projecting from the inner wall and lying close together like the leaves of a book (Figs. 9 and 11). The lamellæ are found mostly upon the flattened cranial and caudal surfaces of the sac. The lateral or distal end of the sac is but slightly encroached upon by them. The medial end shows a smooth lenticular space around the internal gill opening with its long axis dorso-ventrad. From the edge of this space the lamellæ extend toward the external gill opening. Those at the middle of the caudal and cranial walls of the gill sac (*i. e.*, those lying in a direct line between the gill openings) are the longest. Thence they diminish in length dorsally and ventrally on both sides until those near the dorsal and ventral borders of the gill sac are only about 5



mm. in length. The gill lamellæ do not reach the external opening hence there is left a smooth space about the opening. This space is much wider than the one found about the internal gill opening and extends farther along the dorsal and ventral borders (Figs. 9 and 10).

The lamellæ are attached by one margin along their whole length except near the external gill opening. Here they are broadened abruptly and their ends are free. These enlarged free ends of the lamellæ are somewhat triangular and are bent dorsad or ventrad so that they overlap each other along the edge of

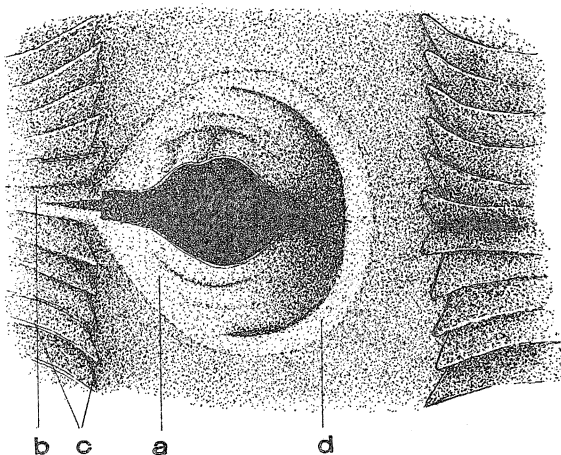


FIG. 9. A portion of the interior of the gill sac showing the external branchiopore with its ental valves in the position they assume when water is entering the gill sac. *a*, ental valve; *b*, central lamellæ which splits and forms the ental valves; *c*, laminae ending free; *d*, cartilaginous ring of the external branchiopore.

the distal smooth area (Figs. 9 and 11). The central lamella on both the cephalic and caudal walls splits into two laminae about 10 mm. from its free ends (Figs. 9 and 11, *b*). The laminae of the cephalic wall end free. When those of the caudal wall reach the edge of the cartilage which surrounds the external gill opening, there extends from each a membranous sheet which forms one of the ental valves (Fig. 9, *a*; Fig. 10, *a*).

Each ental valve is a nearly circular concave plate attached by less than one third of its circumference to the caudal half of the medial end of the external branchiopore. The branchiopore

forms a short tube connecting the gill sac with the exterior. The ental valves extend laterad and at the same time dorsad and ventrad to the outer end of the tubular branchiopore to which the ectal valve is attached. Each has its concave face outward and the two cover about two thirds of the lumen of the branchiopore. Each overlaps its fellow by nearly half its dorso-ventral diameter.

The ectal valve is a thin membrane which is attached to the cephalic half of the outer margin of the external branchiopore and stretches loosely over the cephalic half of its lumen (Fig. 9). The ental valve is attached at the internal

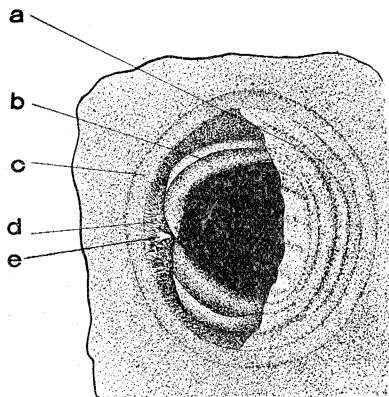


FIG. 10. The external branchiopore showing the normal position of the ectal and ental valves when water is being discharged from the gill sac. *a*, ectal valve; *b*, ental valve; *c*, cartilaginous ring; *d*, buccal fringe; *e*, point on the cartilaginous ring.

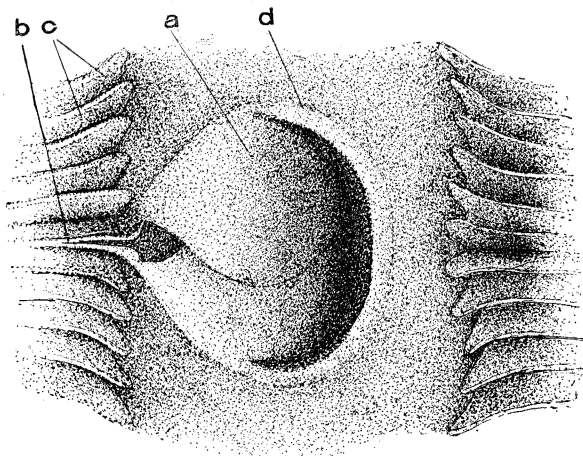


FIG. 11. Position of the ental valves when the ectal valve is stretched taut. *d*, cartilaginous ring; *a*, ental valve; *c*, laminae of the gill sac; *b*, central divided lamellæ.

end of the external branchiopore and on its caudal margin while

the ectal valve is attached to the external end and on the cephalic margin. When the free border of the ectal valve is tightly stretched in the cartilaginous ring (Fig. 12) the ental valves, if forced outward by pressure within the gill sac, strike against the ectal valve and close the external branchiopore thus preventing the escape of water.

If the border of the ectal valve is relaxed it does not afford a support for the ental valves which are then forced out past it by the pressure of the water and thus permit water to pass out through the external branchiopore (Fig. 10). Thus while the valves of the external branchiopore can at no time prevent the entrance of water into the gill sac, they are able under certain conditions, to prevent its exit.

The stretching of the ectal valve is effected by the action of two muscles which elongate the dorso-ventral axis of the cartilaginous ring to which the valve is attached. The first one is seen when the integument is removed and lies on the cranial side of the gill cleft. This small band of muscles lies loosely around the cephalic side of the gill opening, and is attached to the longitudinal bars immediately dorsal and ventral to the vertical axis of the opening and to the ring of cartilage (Fig. 13). This may

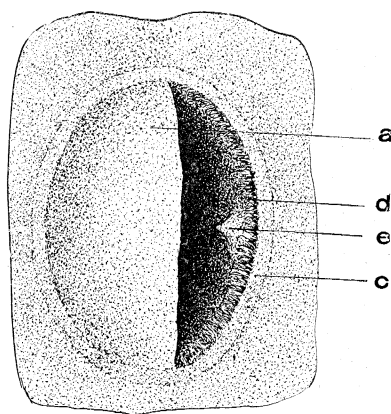


FIG. 12. The cartilaginous ring of the external branchiopore is oval in shape thus stretching the ectal valve taut. *a*, ectal valve; *d*, buccal fringe; *e*, point on the cartilaginous ring; *c*, cartilaginous ring. Figs. 11 and 12, placed back to back as here printed, form together a model of a left external branchiopore with closed valves.

be called the *ectal muscle*.

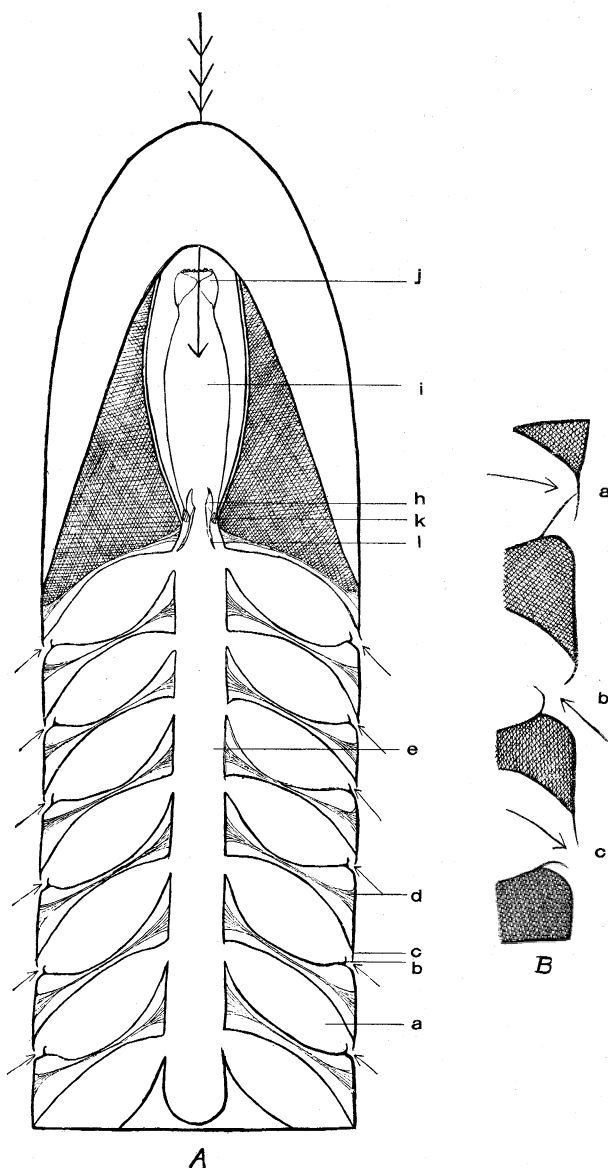


FIG. 13, *A*. A diagram of the respiratory apparatus of *P. marinus*. The possibility of the water entering the gills from the mouth and the external branchiopores at the same time is shown. *a*, gill sac; *b*, ental valve; *c*, ectal valve; *d*, muscular gill-pouch; *e*, water tube; *i*, velar valve; *k*, posterior pharyngeal muscle; *h*, velar jaws; *j*, tongue; *j*, tongue lobe.

FIG. 13, *B*. Diagram of the ectal and ental valves of the external branchiopores of *P. marinus*. *a*, closed valves; *b*, position of valves as water enters the gill; *c*, position of valves when water leaves the gill.

The other half-ring shaped muscle (*ental muscle*) is smaller and extends loosely around the caudal side of the gill sac near its external opening but between the gill sac and its pouch. Thus it cannot be seen unless the muscular pouch be cut and reflected. It is attached to the same longitudinal rods of cartilage as is the ectal muscle, a little beneath the points of attachment of the latter and is attached slightly to the ring of cartilage (Fig. 8, *c*) which sends out a flat semicircular projection. This

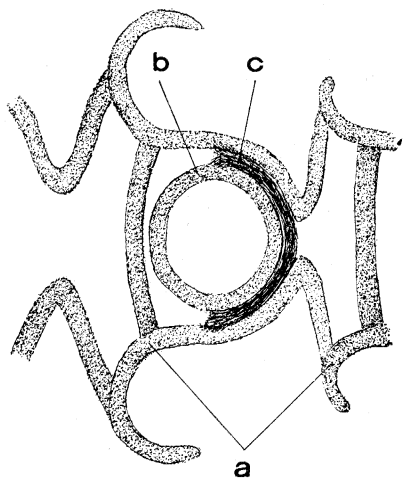


FIG. 14. The ectal muscle and its attachment. *a*, cartilaginous bars; *b*, cartilaginous ring; *c*, ectal muscle.

projection lies on the caudal side of the external gill opening within the ring of cartilage. It bears a slender conical rod of cartilage (Figs. 10 and 12, *e*).

The ectal and ental muscles are striated and function in compressing the sides of the ring of cartilage so that the naturally circular cartilage becomes elliptical with its long axis dorso ventrad. Cuvier (1840) and Mayer (1835) speak of a circular muscle of the gill opening which lies around the ring of cartilage

and serves to close the gill opening. Just how a constrictor muscle, if such a muscle were present, could so compress the cartilaginous ring as to completely close the opening is not clear.

A fringe of hair-like processes lying around the caudal border of the external gill opening deserves mention. Cephalad about 1 mm. from the middle of this fringe is the small cartilaginous projection which is the outgrowth of the cartilaginous ring before mentioned. The function of these outgrowths is not known. They may be tactile.

**D. Nasal Sac.** — The nostril is situated on the dorsal side of the head in the median line about 5 mm. anterior to the paired eyes. This nostril leads into a tube which opens directly into the nasal sac with its olfactory lamellæ. From the cranial por-

tion of the nasal sac there continues ventro-caudad the nasal cœcum which curves around the anterior ends of the brain and notochord (Fig. 1, *f*). This nasal cœcum lies directly under the notochord and ends blindly on a line with the center of the second gill sac. The ventral wall of the tube follows the ethmoid cartilage to its posterior end and is there attached to the pharyngeus muscle as was before noted. It continues caudad from this point. At its caudal end it is parallel to the long axis of the body. The posterior part of the tube which is immediately above the œsophagus, overlies both its dorsal and lateral walls and rests on the first and second gill sacs for 1 or 2 mm. on each side (Fig. 1).

The result of the position of the tube directly between the anterior end of the notochord and the strong muscles of the gill pouch ventral to it is that it is pressed up against the notochord at every contraction of the underlying muscles. This action of the muscles causes the water in the tube to be forced out of the nostril with considerable force. Upon the relaxation of the muscles to which the tube is attached the sac refills (Fig. 1). Thus, although the nasal tube has no direct communication with the respiratory apparatus, yet the effect is practically as though it had. At every expiration from the gills there is a corresponding expiration from the nostril and with every inspiration water passes into the nostril. The relationship existing between the expired and inspired streams of the nostril and gills has long been known, but hitherto the causes underlying this relationship have not been understood.

*(To be continued.)*